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Revision of the dune-associated stiletto flies of the genus *Neotherevella* Lyneborg, 1978 (Therevidae, Therevinae)

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Abstract

The genus *Neotherevella* Lyneborg, 1978 is revised. Two new species are described from Morocco (*Neotherevella maroccanus* **sp. nov.**) and South Africa (*Neotherevella londti* **sp. nov.**), the latter named in honour of the South African Dipterist, Jason G.H. Londt.

Keywords

Asiloidea, Diptera, South Africa

Introduction

Stiletto flies (Therevidae) are found in all biogeographical major regions of world, but are particularly species-rich in Mediterranean and arid environments, where sandy soils are a preferred larval habitat (Holston 2005). In sandy regions, including coastal and desert dune systems, therevids are diverse with some genera specifically adapted to such habitats (Lyneborg 1968; Holston and Almeida 2020). One group of genera in the subfamily Therevinae appears to represent a monophyletic group of dune associates

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and includes *Aristothereva* Frey, 1921, *Acantothereva* Séguy, 1935 and *Neotherevella* Lyneborg, 1978. This clade also contains genera that are frequently encountered in forest habitats with sandy soils, including *Acrosathe* Irwin & Lyneborg, 1981, *Irwiniella*, Lyneborg, 1976 and *Sinothereva* Winterton, 2020 (Holston et al. 2007; Winterton 2020). Moreover, adult stiletto flies associated with dune systems frequently have a peculiar set of morphological characteristics including pale vestiture composed of dense, erect, scale-like setae, small pulvilli, elongate tibial macrosetae and claws and opaque, white wings with dark maculation (Lyneborg 1968; Hauser and Irwin 2003; Holston 2009; Holston and Almeida 2020; Irwin and Winterton 2020, 2021). This morphological body type is seen in *Aristothereva*, *Acantothereva* and *Neotherevella*, but is also exhibited repeatedly in various distantly related genera in other subfamilies, presumably as an adaptation to living in arid, dune habitats (e.g. *Ammonaios* Irwin & Lyneborg, 1981, *Argolepida* Metz & Irwin in Metz et al. 2003, *Orthactia* Kröber, 1912a and some species of *Entesia* Oldroyd, 1968).

Neotherevella is a small genus with a wide distribution throughout the southern Palaearctic Region, as well as disparately in south-western Africa (Lyneborg 1978). With the inclusion of the two new species described herein, the genus contains five species, three in the Palaearctic and two in the Afrotropical Region. We describe two new species of *Neotherevella* from Morocco (*N. maroccanus* sp. nov.) and South Africa (*N. londti* sp. nov.). All species of *Neotherevella* are diagnosed and figured and a key to species presented.

Materials and methods

Terminology follows Cumming and Wood (2017) with additional therevid-specific genitalic morphology according to Winterton et al. (1999a, b). Genitalia were macerated in lactic acid or potassium hydroxide to remove soft tissue, then rinsed in distilled water (neutralised with acetic acid as needed) and dissected in 80% ethanol. Genitalia preparations were placed in glycerine in a genitalia vial and mounted on the pin beneath each specimen. Specimen images were taken at different focal points using a digital camera and subsequently combined into a serial montage image using Helicon Focus (HeliconSoft Ltd., Kharkiv, Ukraine). All new nomenclatural acts are registered in Zoobank (Pyle and Michel 2013). Descriptions were composed using a character matrix in Lucid Builder 3.5 (Identic Pty. Ltd., Brisbane, Australia) and exported as natural language descriptions in XML and text format. Some specimens have various data contained in a specimen database 'Mandala' (Kampmeier and Irwin 2009) and have unique numbers on separate yellow labels stating: "ME Irwin Therevidae Specimen # MEI99999". Geospatial coordinates, either included on the original collection label or approximated *a posteriori*, are listed in brackets. Collection depositories from which specimens were examined: American Museum of Natural History, New York, USA (AMNH); Canadian National Collection, Ottawa, Canada (CNC); California State Collection of Arthropods, Sacramento, USA (CSCA); The Natural History Museum,

London, United Kingdom (NHM); KwaZulu-Natal Museum, Pietermaritzburg, South Africa (NMSA); Royal Belgian Institute of Natural Sciences, Brussels, Belgium (RBINS); Senckenberg Natural History Museum, Frankfurt, Germany (SMF); Smithsonian National Museum of Natural History, Washington D.C., USA (USNM); Zoological Institute of Russian Academy of Sciences, St. Petersburg (ZISP); Museum für Naturkunde, Berlin, Germany (ZMHB).

Results

Neotherevella Lyneborg

Neotherevella Lyneborg, 1978: 75— Lyneborg (1980: 319 [catalogue]), (1989: 22 [catalogue]); Majer (1997: 527 [key]); Hauser et al. (2017: 1200 [key, synopsis]). Type species: *Thereva citrina* Becker, 1902: 35.

Neothereva Kröber, 1912b: 138, *sensu* Lyneborg (1976: 291), *nec* Kröber (1937: 276). Type species: *Thereva citrina* Becker, 1902: 35 [incorrect type species designation by Lyneborg (1976)].

Diagnosis. Extensive erect, white setae on head, body and legs; female frons wide, inner eye margins subparallel to slightly divergent; parafacial setae absent; hind coxal knob relatively minute or absent; elongate macrosetae on tibia and tarsi; series of anteroventral macrosetae on hind femur; wing opaque white with brown markings; male distiphallus narrow, short.

Description. Small to medium-sized flies extensively covered with erect, elongate pile. Head length and height subequal; frons flat, grey pubescent with pair of large matte black pubescent spots in female (rarely in male); vertex sunken (especially in female); inner margins of female eyes subparallel; gena rounded; male frons width variable, contiguous below anterior ocellus to wider than ocellar tubercle; frons width strongly sexually dimorphic; parafacial without setae; face flat; occiput pubescence dull silver to grey-brown, postocular ridge and occiput in both sexes with macrosetae few in number, single row or irregularly arranged; antenna shorter than to subequal to head length, positioned on lower half of head and directed anteriorly; flagellum shape variable, cylindrical (slightly tapered distally), elliptical or conical, length shorter than or subequal to combined scape and pedicel length, style apical; scape short, less than 3× pedicel length, cylindrical, noticeably thicker than pedicel and base of flagellum; palpus slender or crassate, mouthparts short. Thorax with central depression of prosternum setose; cervical sclerite lacking macroseta; pleuron with silver pubescence admixed with erect, filiform and lanceolate setae; metanepisternum with postspiracular setae present; metakatepisternum setae absent; scutum covered with lanceolate and filiform adpressed setae, often of variable length and white; scutal chaetotaxy (pairs of macrosetae): notopleural, 3–5; supra alar, 1– 2; post alar, 1; dorsocentral 0–6; scutellar, 2; posterior surfaces of mid- and hind coxae setose, hind coxal knob absent or reduced

in size; all legs approximately equal length; fore and mid-femoral anteroventral (av) macrosetae present or absent, hind femur with anteroventral (av) setae as series along segment, posteroventral (pv) macrosetae present or absent; femoral vestiture as filiform setae admixed with adpressed, lanceolate and scale-like setae; tibial macrosetae elongate; claws relatively small; wing cell m_3 open or closed; wing white opaque with variable mottled pattern; vein R_1 with setae absent (rarely single seta present); wing membrane densely covered with microtrichia. Abdomen shape relatively short or elongate, slightly narrowed along length. Male terminalia with gonocoxites separate medially, posteromedial margins proximal; inner gonocoxal process (igp) present, articulated; posterior outer gonocoxal process (ogp) barely evident; ventral lobe elongate, half the length of gonostylus; phallus with dorsal apodeme of parameral sheath broad, covering aedeagus dorsally or quadrangular, dorsal apodeme separate from gonocoxites, distiphallus narrow, short and directed ventrally, ventral apodeme as single lobe, narrow. Female terminalia with acanthophorite setae present as two sets (A1 and A2), A1 enlarged and elongate; sternite 8 emarginate posteromedially; tergite 8 elongate with anteromedial process; spermathecal sac as single round lobe, two round spermathecae.

Included species. *Neotherevella arenaria* (Lyneborg, 1976), *N. kozlovi* (Zaitzev, 1971a), *N. londti* sp. nov., *N. macularis* (Wiedemann, 1828), *N. maroccanus* sp. nov.

Comments. *Neotherevella* was described by Lyneborg (1978) as a clarification of the confused taxonomic concept of the genus *Neothereva* Kröber, 1912b, itself being a heterogeneous composite of species now placed in *Neotherevella* and *Thereva* — the latter of which *Neothereva* is arguably a synonym (see Lyneborg 1976, 1978). Kröber (1912b) described *Neothereva* with five Palaearctic species: *N. nitidifrons* Kröber, 1912b; *N. angustifrons*, 1912b; *N. latifrons* (Macquart, 1848); *N. citrina* (Becker, 1902) and *N. frontata* Kröber, 1912b. Lyneborg (1976) noted that the essential distinction between *Thereva* and *Neothereva* by Kröber (1912b) was that the male eyes are widely separated. Kröber (1929, 1932, 1937) subsequently identified multiple synonyms or novel combinations, as well as including *Neothereva* as a subgenus of *Thereva* (Kröber, 1932). In a catalogue of Palaearctic Therevidae, Kröber (1937) designated *N. nitidifrons* as the type species of *Neothereva*. In his revision of the Afrotropical Therevidae, Lyneborg (1976) overlooked this type species designation and incorrectly designated *N. citrina* (Becker, 1902) as the type species of the genus. Therein, *T. frontata* and *T. nitidifrons* were moved to *Thereva*, *T. latifrons* implied as a *nomen dubium*, while *Neothereva* was more narrowly circumscribed around *N. citrina* along with the newly-described *N. arenaria*. Lyneborg (1976) also synonymised *N. angustifrons* with *N. citrina* and *Thereva macularis* Wiedemann, 1828 was moved to *Neothereva*. Recognising his previously incorrect type species designation for *Neothereva*, Lyneborg (1978) synonymised *Neothereva* (*sensu* Kröber, 1937) with *Thereva* and transferred *N. arenaria*, *N. citrina* and *N. macularis* to a new genus *Neotherevella* (again based on the type species as *T. citrina*) along with a species described previously in *Aristothereva* (*A. kozlovi* Zaitzev, 1971a).

Neotherevella, *Aristothereva* and *Acantothereva* form a closely related group of specialised genera associated with sandy habitats, especially dunes, that is part of a larger clade also comprising the species-rich and widely distributed genera *Irwiniella* and

Acrosathe (see Holston et al. 2007; Holston 2009; Winterton et al. 2016). *Neotherevella* is differentiated from other therevine genera by the presence of paired dark maculae on a wide female frons (also in the male of *N. londti* sp. nov.), parafacial setae absent (present in *Acrosathe* and *Acantothereva*, variable in *Aristothereva*) and a distiphallus that is narrow and curved ventrally (bulbous in *Acantothereva*; ornately spinose in *Aristothereva*). Other features of this genus variably shared with *Acantothereva* and *Aristothereva* include a wide, sunken vertex (especially in females), opaque white wings with dark maculation, reduced hind coxal knob, elongate tibial macrosetae and extensive white pile on the head and body frequently admixed with white scale-like setae. Paired matte-black pubescent maculae on the female frons are present in all species of *Neotherevella*, but are also found in some species of *Acrosathe* (for example, notably *Acrosathe vialis* (Osten Sacken, 1877), suggestive also of the close relationship of these genera.

Neotherevella is widely distributed throughout the Palaearctic Region and disparately in southern Africa. The most eastern species, *N. kozlovi*, is recorded from China and Uzbekistan. In the Mediterranean Region, *N. macularis* is widely distributed throughout northern Africa from Israel to Mauritania; the apparently closely related and distinctively coloured *N. maroccanus* sp. nov. is known only from Morocco.

Key to species of *Neotherevella*

1 Macrosetae on head, thorax and legs black; matte-black pubescent spots on female frons admixed with erect black setae (southern Africa) **2**

– Macrosetae on head, thorax and legs pale yellow to white, barely distinguishable from extensive white pile; matte-black pubescent spots on female frons without setae (northern Africa to Mongolia) **3**

2 Wing cell m_3 open; palpi crassate; all femora with ventral macrosetae; male eyes separated by distance greater than width of ocellar tubercle; male frons with two matte- black spots admixed with elongate, erect setae (South Africa)..... ***Neotherevella londti* sp. nov**

– Wing cell m_3 closed; palpi slender; only hind femur with ventral macrosetae; male eyes almost contiguous below anterior ocellus; male frons lacking matte-black spots (Namibia) ..... ***Neotherevella arenaria* (Lyneborg)**

3 Wing cell m_3 open; male eyes separated by distance greater than width of ocellar tubercle (China, Uzbekistan) ..... ***Neotherevella kozlovi* (Zaitzev)**

– Wing cell m_3 closed; male eyes separated by distance less than width of ocellar tubercle (northern Africa, Middle East) **4**

4 Male eyes contiguous below anterior ocellus; male covered with extensive yellow pile on scutum, dorsal portion of occiput and dorsally on abdomen, white pile on pleuron lower half of head and laterally on abdomen; flagellum narrow (Morocco) (female unknown)..... ***Neotherevella maroccanus* sp. nov.**

– Male eyes separated at narrowest point by width subequal to width of ocellar tubercle; uniform white pile on head, thorax and abdomen; flagellum conical, tapered (Mauritania to Israel, Sudan) ... ***Neotherevella macularis* (Wiedemann)**

***Neotherevella arenaria* (Lyneborg)**
Figs 1–3, 11C, D, 12A, B, 13A, B, 14B, 15

Neothereva arenaria Lyneborg, 1976: 293.
Neotherevella arenaria (Lyneborg, 1976)— Lyneborg (1978: 76 [combination change], 1980: 319 [catalogue]); Hauser et al. (2017: 1200 [faunal synopsis, wing figure]).

Holotype. Namibia • male; **Erongo Region**, Swakopmund; 26–30 Jan 1972; NHM.

Other material. Namibia • 8 males, 7 females; **Erongo Region**, Swakopmund, Swakop River mouth; [-22.6886, 14.5275]; 8 m alt.; 9 Feb 1974; M.E. & B.J. Irwin leg.; coastal and riverbed dunes; CSCA; MEI028397–400, 120720–23, 120760–1, 178074–8 • 3 males; **Erongo Region**, Swakopmund, Swakop River mouth; [-22.6925, 14.5269]; 03 Feb 2012; T. Dikow leg.; sandy river bed and vegetated dunes; USNM; USNMENT01576797–9 • 2 males, 1 female; **Karas Region**; Lüderitz District, Agate Beach, 10 km N Lüderitz; [-26.5949, 15.1792]; 3 m alt.; 18 Feb 1974; M.E. & B.J. Irwin leg.; low coastal vegetated dunes; CSCA; MEI120715, 178075–6.

Diagnosis. Male frons lacking dark maculae; female frontal maculae with short pile of erect macrosetae; male eyes contiguous below ocellar tubercle; wing cell m_3 closed; all macrosetae black; single pair (sometimes two) of dorsocentral macrosetae; palpus slender.

Redescription. Body length: 6.0–6.5 mm (male), 7.0–7.5 mm (female). ***Head.*** Frons profile flat, wholly pubescent; male frons narrower than anterior ocellus, but eyes not contiguous, female frons broad with eyes slightly narrowed dorsally; frontal pubescence silver with dark yellow suffusion, female with paired matte-black maculae admixed with short, erect, black setae; male frons with small patch of short setae above antenna, female sparse short setae, frontal setae admixed black and yellow; postocular setae black, arranged in single row immediately laterad of ocellar tubercle (male), additional setae irregularly arranged medially (female); occiput relatively flat, silver pubescence admixed with white, scale-like setae, more abundant medially; genal setae pale, palpus narrow, covered with pale setae; antennal scape shorter than flagellum, slightly thickened and cylindrical, brown, overlain with grey pubescence admixed with erect black setae of varying lengths; flagellum conical, brown with grey pubescence. ***Thorax.*** Scutum grey-tan with brown markings, short erect filiform setae admixed with adpressed white scale-like setae, denser anteriorly; macrosetae black; scutellum concolourous with scutum; pleuron with dense silver-grey pubescence admixed with extensive semi-erect, white, scale-like setae; anepisternum with brownish suffusion dorsally; coxae with pale macrosetae admixed with erect white, scale-like setae; femora with dense covering of white, scale-like, adpressed setae (sparser in female); legs dark yellow, macrosetae black; hind femur with 3–4 anteroventral macrosetae distributed along distal half; tarsi dark yellow with apices brown; tibial and tarsal macrosetae elongate; wing white with irregular-sized brown maculae (darker in female), spur veins often present in maculae; cell m_3 closed; wing venation yellow basally along major veins, darker distally; haltere dark yellow; scutal chaetotaxy (macrosetae pairs): notopleural, 3; supra alar, 1–2; post alar, 1; dorsocentral, 1–2;

Figure 1. *Neotherevella arenaria* (Lyneborg, 1976), female **A** oblique view **B** lateral view.

Figure 2. *Neotherevella arenaria* (Lyneborg, 1976), male **A** oblique view **B** lateral view.

scutellar, 2. ***Abdomen***. Male base colour yellow, grey pubescent, filiform setae admixed with adpressed setae, very dense in male; terminalia dark yellow; female abdomen dark yellow; acanthophorite spines black. ***Male genitalia***. Epandrium sub-quadrangular, posterolateral corners thickened, rounded; sternite 8 rounded posteriorly with thickened margin and short series of elongate, marginal macrosetae; gonocoxite with extensive pale setae, outer gonocoxal process relatively narrow, angular; gonocoxal apodeme absent; inner gonocoxal process rounded apically; gonostylus narrow; ventral lobe short, rounded; distiphallus narrow, gradually curved ventrally; ventral apodeme triangular.

Distribution. Coastal Namibia.

Ecology. *Neotherevella arenaria* sp. nov. adults are found in coastal dune systems associated with low vegetation (Fig. 3).

Conservation status. Unknown; this species is apparently locally abundant in relatively undisturbed habitats.

Comments. *Neotherevella arenaria* sp. nov. is closely related to *N. londti* sp. nov. and represents a species pair sharing characters not found in other *Neotherevella* species, including erect macrosetae on the frontal maculae, black thoracic macrosetae (pale in other species) and distinct dorsocentral macrosetae (absent or indistinct in other species). These two species are found in south-western Africa, relatively disparately distributed from other *Neotherevella* species, which are found throughout the southern Palaearctic Region.

Figure 3. Vegetated sand dunes at the Swakop River mouth, Swakopmund (Namibia); habitat of *Neotherevella arenaria* (photo copyright: Torsten Dikow).

***Neotherevella kozlovi* (Zaitzev)**
Figs 4, 11A, B, 12C, D, 13C, D, 14A, 15

Aristothereva kozlovi Zaitzev, 1971a: 66— Zaitzev (1971b: 39 [key]); Gorodkov et al. (1974: 226 [faunal record]).
Neotherevella kozlovi Zaitzev (1971a)— Lyneborg (1978: 76 [new combination]; 1989: 22 [catalogue]).

Holotype. Peoples Republic Of China • male; **Inner Mongolia**, Etsin Gol, North Alashan, Gobi; [41.8056, 100.9883]; 23 Jun 1926; P. Kozlov leg.; ZISP; N2236.

Paratypes. Peoples Republic Of China • 3 males, 6 females; **Inner Mongolia,** same data as holotype; [41.8056, 100.9883]; 14–15 Mar 1908, 23 Jun 1926; P. Kozlov leg.; ZISP, CSCA. Uzbekistan • 1 female; **Xorazm Region**, Khiva; [41.3847, 60.3655]; 20 Apr 1927; L. Zimin leg.; ZISP.

Diagnosis. Male frons lacking dark maculae, wider than ocellar tubercle at narrowest point; female frontal maculae without erect macrosetae; scape macrosetae white to yellow; palpus narrow; wing cell m_3 open; all macrosetae yellow-white; dorsocentral macrosetae absent.

Redescription. Body length: 8.0 mm (male), 10.5 mm (female). ***Head***. Frons profile flat to slightly rounded (female), male frons width at narrowest point slightly wider than ocellar tubercle, female frons wide, inner eye margins subparallel; pubescence greyish-silver, paired matte-black pubescent maculae present (female), male frons with setae absent, female frons with patch of pale setae beside and slightly below antennal base; postocular setae white, arranged in single row, occiput relatively convex, pubescence grey admixed with white, scale-like setae, abundant medially; genal setae pale; palpus narrow, with white setae; antennal scape bulbous, equal length to flagellum, brown, overlain with grey pubescence (male) or dark yellow-orange, overlain with grey pubescence (female), numerous large white-yellow setae; flagellum brown. ***Thorax***. Scutum grey pubescent, erect, filiform setae admixed with adpressed, white, scale-like setae, denser anteriorly; thoracic macrosetae yellow; scutellum concolourous with scutum; pleuron with dense silver-grey pubescence admixed with extensive semi-erect, white, scale-like setae; coxae yellow, overlain with silver-grey pubescence, macrosetae few in number, setae white; femora uniform yellow (female) or dark grey-brown with apices yellow (male), dense covering of white, scale-like adpressed setae, macrosetae white, hind femur with 3–4 anteroventral macrosetae in distal half; tibiae and tarsi dark yellow, macrosetae elongate, white; wing opaque white, brown along veins; cell m_3 open; venation yellow basally along major veins, darker distally; haltere dark yellow; scutal chaetotaxy: notopleural, 5; supra alar, 1; post alar, 2; dorsocentral, 0; scutellar, 2. ***Abdomen***. Male base colour grey pubescent with extensive long, pale filiform setae admixed with adpressed setae; terminalia dark yellow; female abdomen brown, tergites yellow posteriorly and laterally; acanthophorite spines yellow. ***Male genitalia***. Epandrium ovoid, brown

Figure 4. *Neotherevella kozlovi* (Zaitzev, 1971) **A** female, lateral view **B** male, oblique view.

anteromedially, covered with pale setae, corners pointed posterolaterally; sternite 8 narrowed posteriorly, emarginate apically with elongate setae in posterior half; gonocoxites with dense white setae, outer gonocoxal process reduced to small ridge, inner gonocoxal process narrowed apically, gonostylus truncated apically, angular ridge on outer surface, ventral lobe relatively large, rounded; gonocoxal apodeme small; phallus with broad dorsal apodeme of parameral sheath, ventral apodeme triangular, distiphallus broad and curved ventrally.

Distribution. China (Inner Mongolia), Uzbekistan.

Ecology. *Neotherevella kozlovi* adults are found in sand dunes habitats.

Conservation status. Not threatened; apparently widely distributed in relatively undisturbed areas.

Comments. *Neotherevella kozlovi* was originally described in *Aristothereva* by Zaitzev (1971a) and later transferred to *Neotherevella* by Lyneborg (1978). The presence of distinctive frontal maculae of the female frons supports this combination. This species is distinct from other *Neotherevella* species by the shape of the frons in both sexes and yellow scape macrosetae.

***Neotherevella londti* sp. nov.**

https://zoobank.org/167C5044-7846-48EC-8D75-233077B9125C

Figs 5–7, 11E, F, 12E, F, 13E, F, 14C, E, 15

Holotype. South Africa • male; **Western Cape Province**, Cape Vermont, nr. Onrus; [-34.4013, 19.1352]; 6 Apr 1979; J. Londt & B. Stuckenberg leg.; dune vegetation and sandy road; 3419AC; NMSA; MEI115849.

Paratypes. South Africa • 3 males, 7 females; **Western Cape Province**, same data as holotype; NMSA, CSCA; MEI115850–6, 115857–9. • 3 females; **Western Cape Province**, Glencairn, pres. Simonstown; [-34.1646, 18.4291]; M. Bequaert leg.; R.I.Sc.N.B., 24.236; RBINS. • 5 males; **Western Cape Province**, Fish Hoek; M. Bequaert leg.; [-34.1449, 18.4323]; R.I.Sc.N.B,. 24.236; RBINS.

Diagnosis. Male frons with dark maculae present, frontal maculae with elongate pile of erect macrosetae, male frons wider than ocellar tubercle at narrowest point; cell m_3 open; all macrosetae black, elongate and numerous; two pairs of dorsocentral macrosetae; palpi crassate and acuminate; all femora with ventral macrosetae.

Description. Body length: 8.0–8.5 mm (male), 7.5–8.5 mm (female). ***Head***. Frons profile flat, wholly pubescent; vertex excavated (more so in male); male frons slightly wider than ocellar tubercle at narrowest point, female frons broad with eyes slightly narrowed dorsally; frontal pubescence silver ventrally, grey-tan dorsally, paired matte-black maculae with erect black setae (longer in male); postocular setae black, elongate, strongly curved anteriorly in a single row, additional setae irregularly arranged medially on occiput; male occiput relatively concave, pubescence silver with scale-like setae medially; antennal scape slightly longer than flagellum, slightly thickened, cylindrical, brown, overlain with grey pubescence, densely covered with large, dark setae; flagellum brownish-orange, darker distally; genal setae dark; palpus crassate, acuminate with extensive erect white and black setae. ***Thorax***. Scutum pubescence grey-tan with brown mottling, erect filiform setae admixed with adpressed, white, scale-like setae, denser anteriorly (longer in male), thoracic macrosetae black and relatively elongate; scutellum concolourous with scutum; pleuron with dense silver-grey pubescence admixed with extensive, semi-erect, white, scale-like setae; anepisternum with brownish suffusion dorsally;

Figure 5. *Neotherevella londti* sp. nov., female **A** oblique view **B** lateral view.

Figure 6. *Neotherevella londti* sp. nov., male **A** oblique view **B** lateral view.

Figure 7. *Neotherevella londti* sp. nov. **A** male head, lateral view **B** female head, lateral view.

coxae dark, overlain with silver-grey pubescence, setae white and black, macrosetae numerous, strong, black; femora dark brown, short black setae admixed with longer setae, sparse covering of white scale-like adpressed setae (denser in male), all femoral anteroventral and posteroventral macrosetae black, more numerous on hind femur, hind femur with 3–12 anteroventral macrosetae along entire length; tibiae and tarsi brown, macrosetae elongate, black; wing opaque yellow-tan and white with irregular dark brown markings in most cells; some individuals with a short, black macroseta distally on R_1; cell m_3 open; venation yellow basally along major veins, darker distally; haltere stem pale with knob mostly brown; scutal chaetotaxy: notopleural, 3; supra alar, 2; post alar, 1; dorsocentral, 2; scutellar, 2. ***Abdomen***. Abdomen dark brown dorsally, grey pubescent laterally, dense pile of filiform erect and adpressed, scale-like setae, brown medially, white marginally on all tergites, denser laterally and posteriorly; female abdomen similar to male, except setal pile much sparser; acanthophorite spines black. ***Male genitalia***. Dark brown with brown setae; epandrium sub-quadrangular, posterior margin thickened and posterolateral corners rounded; sternite 8 ovoid; gonocoxites with outer gonocoxite process relatively short, truncated; gonocoxal apodeme narrow; inner gonocoxal process rounded apically; gonostylus with small angular ridge medially; ventral lobe relatively large and spatulate; phallus with dorsal apodeme broad, ventral apodeme triangular; distiphallus narrow.

Etymology. This species is named in honour of Jason Londt, who, along with Brian R. Stuckenberg, collected most of the known specimens.

Distribution. South-western South Africa.

Ecology. *Neotherevella londti* sp. nov. adults were collected on vegetated coastal sand dunes.

Conservation status. Unknown; this species is known from two small series of specimens from a relatively small area in Western Cape region. The type locality has residential developments along the coast in dune habitats where this species is known.

Comments. *Neotherevella londti* sp. nov. is unique in the genus in having crassate palpi, frontal maculae in both sexes and extensive dark, elongate macrosetae on the head, body and legs. Some individuals have a small macroseta present distally on wing vein R_1, a feature found disparately in some distantly-related genera.

Neotherevella macularis (Wiedemann)

Figs 8, 9, 11G, H, 12G, H, 13G, H, 14D, F, 15

Thereva macularis Wiedemann, 1828: 558— Bezzi (1903: 209 [catalogue], 1906: 264 [catalogue]); Kertész (1909: 155 [catalogue]); Kröber (1912c: 254 [checklist], 1912d: 409 [redescription], 1913: 49, 58 [key, checklist], 1924a: 100 [possible synonymy], 1924b: 17 [synonymy]).

Neothereva macularis (Wiedemann, 1828)— Kröber (1937: 276 [combination change, catalogue]); Lyneborg (1976: 294 [redescription]); Steyskal & El-Bialy (1967: 53 [checklist]).

Figure 8. *Neotherevella macularis* (Wiedemann, 1828), female **A** oblique view **B** lateral view.

Neotherevella macularis (Wiedemann, 1828)— Lyneborg (1978: 76 [combination change], 1980: 319 [catalogue], 1989: 22 [catalogue]); El-Hawagry et al. (2011: 152 [catalogue]; Kettani et al. (2022: 213 [catalogue]).

Thereva citrina Becker, 1902: 35— Bezzi (1903: 208 [catalogue], 1906: 264 [catalogue]); Kertész (1909: 152 [catalogue]). syn. nov.

Neothereva citrina (Becker, 1902)— Kröber (1912b: 138, 139 [key, redescription], 1913: 42 [key, checklist], 1924a: 17 [key redescription], 1937: 276 [catalogue]).

Neotherevella citrina (Becker, 1902)— Lyneborg (1978: 76 [combination change], 1989: 22 [catalogue]); El Hawagry et al. (2011: 151 [catalogue]).

Neothereva angustifrons Kröber, 1912b: 139— Kröber (1913: 42 [key, checklist], 1924a: 100 [redescription, antennae figure], 1924b: 17 [key, redescription], 1929: 75 [catalogue, possible synonymy]).

Type material. *Thereva macularis* Wiedemann, 1828— ***Holotype*** Sudan • female; Abyssina; Dr. Rüppell; SMF. *Thereva citrina* Becker, 1902— ***Lectotype*** Egypt • male; ZMHB. *Neothereva angustifrons* Kröber, 1912b— ***Holotype*** Egypt • male; ZMHB.

Other material. Egypt • 1 male, 1 female; **Giza Governorate**, Abu [Abou] Rowash; [30.0451, 31.0899]; 12 Sep 1924, 11 Mar 1925; Min. Agric. (Egypt), R.M. leg.; AMNH; MEI084347–8. Israel • 7 males, 1 female; **Haifa District**, Sdor Yam (nr. Caesarea); [32.4831, 34.8985]; 30 m alt.; 14 Apr 1995; M.E. Irwin leg.; shifting coastal dunes; CSCA; MEI028294–5, 02827, 030658, 030661–2, 030667, 060671 • 2 males, 1 female; **Southern District**, Nizzamin [Nitsanim] Beach; [31.7368, 34.6148]; 15 Apr 1995; M.E. Irwin leg.; 43 m; shifting coastal dunes; CSCA; MEI030677–8, 030680 • 1 female; **Tel Aviv District**, Holon, nr. Tel Aviv; [31.9999, 34.7793]; 6 Apr 1968; S. Bleszynski leg.; CNC; MEI079732. Tunisia • 1 female; **Kebili Governorate** [Qibili], Jebil National Park; [32.9777, 9.0425]; 5–13 Oct 2010; H. Pohl leg.; sand dunes; CSCA. Morocco • 1 female; **Agadir-ida Ou Tanane Province**, 10 km S Agadir, Tifnit; [30.1972, -9.6383]; 15.IV.2015; Schmid-Egger leg., 43 m; CSCA.

Diagnosis. Male frons lacking dark maculae (small light brown suffused areas present); male frons slightly narrower than ocellar tubercle at narrowest point; female frontal maculae without erect macrosetae; cell m_3 closed; all macrosetae white; dorsocentral macrosetae absent; palpi slender.

Redescription. Body length: 5.5–7.0 mm (male), 7.5–11.0 mm (female). ***Head***. Frons profile flat, pubescence grey, silver ventrally and on face, pair of suffused brown marks dorsally along eye margin (male) or matte-black maculae (female), lacking setae on frons; male frons width at narrowest point slightly wider than anterior ocellus; female frons broad with inner margins of eyes sub-parallel; white postocular setae arranged in single row immediately laterad of ocellar tubercle, barely discernible from pale setae; male occiput relatively convex, pubescence silver admixed with white, scale-like setae abundant medially; antennal scape length equal to flagellum, brown (male) or dark yellow (female), overlain with grey pubescence admixed with numerous large pale macrosetae; flagellum brown; genal setae white, palpi slender,

Figure 9. *Neotherevella macularis* (Wiedemann, 1828), male **A** oblique view **B** lateral view.

setae white. ***Thorax***. Scutum grey, with erect filiform setae admixed with adpressed, white, scale-like setae, denser anteriorly; thoracic macrosetae white to yellow; scutellum concolourous with scutum; pleuron with dense silver-grey pubescence admixed with extensive semi-erect, white, scale-like setae; coxae dark, overlain with silver-grey pubescence, setae white, macrosetae few in number and pale; femora uniform yellow (female) or dark brown (male), dense covering of white, scale-like adpressed setae, macrosetae white; hind femur with 3–4 fine anteroventral macrosetae spaced along entire length; tibiae yellow, dark grey-brown apically (male) or dark yellow (female); tarsi dark yellow, brown apically in male; wing opaque white, brown along veins (darker in female); cell m_3 closed; venation yellow basally along major veins, darker distally; haltere stem orange-brown, knob yellow; scutal chaetotaxy: notopleural, 3; supra alar, 1; post alar, 1; dorsocentral, 0; scutellar, 2. ***Abdomen***. Dark brown, yellow posteriorly on all tergites, pale filiform setae admixed with adpressed, white, scale-like setae (denser in male); terminalia dark yellow; female acanthophorite spines yellow. ***Male genitalia***. Epandrium with extensive pale setae, narrowed posteriorly with posterolateral corners acute and divergent; sternite 8 quadrangular with strongly emarginate posterior margin, elongate pale setae on entire surface; gonocoxites with small ridge-like outer gonocoxal process; inner gonocoxal process narrow; gonostylus with angular ridges along outer surface; phallus with dorsal apodeme broader posteriorly with shoulder like ridges; ventral apodeme broad, triangular; distiphallus short, narrow.

Distribution. Egypt, Israel, Mauritania, Morocco, Sudan, Tunisia.

Ecology. *Neotherevella macularis* adults are found on vegetated sand dunes.

Conservation status. Not threatened; a widely distributed species.

Comments. *Neotherevella macularis* was originally described in the genus *Thereva*, based on a single female specimen from Abyssinia (Sudan), although listed as Egypt by Wiedemann (1828) and Kröber (1912d). Kröber (1912d) and Lyneborg (1976) redescribed this species, noting that, despite the poor condition of the type specimen, it retained the distinctive colouration and markings typical of the genus. The species was transferred to *Neothereva* (*sensu* Lyneborg, 1976) and subsequently to *Neotherevella* by Lyneborg (1978). Lyneborg (1976) redescribed it briefly and compared it with his newly-described *N. arenaria* from southern Africa, although surprisingly not with the geographically nearby *N. citrina*. At the time, the male of *N. macularis* was unknown, but Lyneborg (1976) assumed that it would certainly have the eyes well separated, a character which is indeed typical of *N. citrina*. As mentioned previously, in his revision of *Neothereva*, Lyneborg (1976) incorrectly designated *T. citrina* as the type species of the genus, something he subsequently corrected (Lyneborg 1978) by describing *Neotherevella* and designating *T. citrina* as the type species. Lyneborg (1976) indicated his placement of *T. macularis* in *Neothereva* was novel, apparently being unaware that it had already been proposed by Kröber (1937). Moreover, his synonymy of *N. angustifrons* with *N. macularis* was also not novel, as Kröber (1937) had previously identified *N. angustifrons* as a synonym of

N. macularis along with *T. nuba* Wiedemann, 1828 (the latter species is now placed in *Irwiniella*). Indeed, Kröber (1924b, 1929) suggested that *T. macularis* and his own *N. angustifrons* might be synonymous, although Kröber (1924a) erroneously considered *T. macularis* as a junior synonym of *N. angustifrons*; he later recognised this error and reversed the synonymy (Kröber 1937) as *T. macularis* is the senior name and, thus, takes precedence.

On the status of three names in question (i.e. *T. macularis*, *T. citrina* and *N. angustifrons*), *T. citrina* being a junior synonym of *T. macularis* is the only one that has not been previously proposed. The male is known for *N. citrina* and *N. angustifrons*, but not *N. macularis*, but comparison of types and a series of specimens (males and females) indicates that characters used previously to separate them (notably scutal colour and markings or frontal markings) tend to be highly variable or obscure. Moreover, the recorded distributions of all three overlap: *N. citrina* is recorded from Mauritania to Israel, *N. angustifrons* from Egypt and *N. macularis* from Sudan, Egypt and Mauritania.

Neotherevella macularis can be separated from all other species of *Neotherevella* by the male frons being only slightly wider than the anterior ocellus, wing cell m_3 closed and by the shape of the male epandrium and phallus.

***Neotherevella maroccanus* sp. nov.**

https://zoobank.org/F2CE53CA-52C1-4758-865B-718F442FACB6
Figs 10, 11I, 15

Holotype. Morocco • male; **Drâa-Tafilalet Region**, Merzouga, 45 km S Erfoud; [31.0847, -4.0055]; 19 Nov 1989; M.E. Irwin leg.; sieved from dune sand beneath vegetation, pupated 21 Oct 1990, eclosed 8 Nov 1990; [pupal case attached to pin]; CSCA; MEI120637.

Diagnosis. Male eyes contiguous below ocellar tubercle, male frons lacking dark maculae; wing cell m_3 closed; all macrosetae white; dorsocentral macrosetae absent; palpi slender.

Description. Body length: 7.5 mm (male). ***Head***. Male frons flat in profile, pubescence grey with orange suffusion, setae absent, eyes contiguous below ocellar tubercle; postocular ridge with white macrosetae arranged in single row immediately laterad of ocellar tubercle; male occiput relatively concave, pubescence grey with abundant yellow adpressed scale-like setae over occiput; antennal scape shorter than flagellum, slightly thickened, cylindrical, brown with grey pubescence admixed with numerous large, pale setae; flagellum brown, elongate cylindrical, pale setae basally; genal setae pale, palpi narrow with pale setae. ***Thorax***. Scutal vestiture with yellow, adpressed, scale-like setae abundant, denser laterally and anteriorly; thoracic macrosetae yellow; scutellum similar to scutum; pleuron dark with sparse grey pubescence admixed with extensive semi-erect, white, scale-like setae, yellow on dorsal part on anepisternum;

Figure 10. *Neotherevella maroccanus* sp. nov., male **A** oblique view **B** lateral view.

coxae yellow, overlain with silver-grey pubescence, setae white, coxal macrosetae few in number, white; femora orange, dense covering of adpressed, white, scale-like setae, macrosetae white, hind femur with 1–2 subapical anteroventral macrosetae; tibiae dark

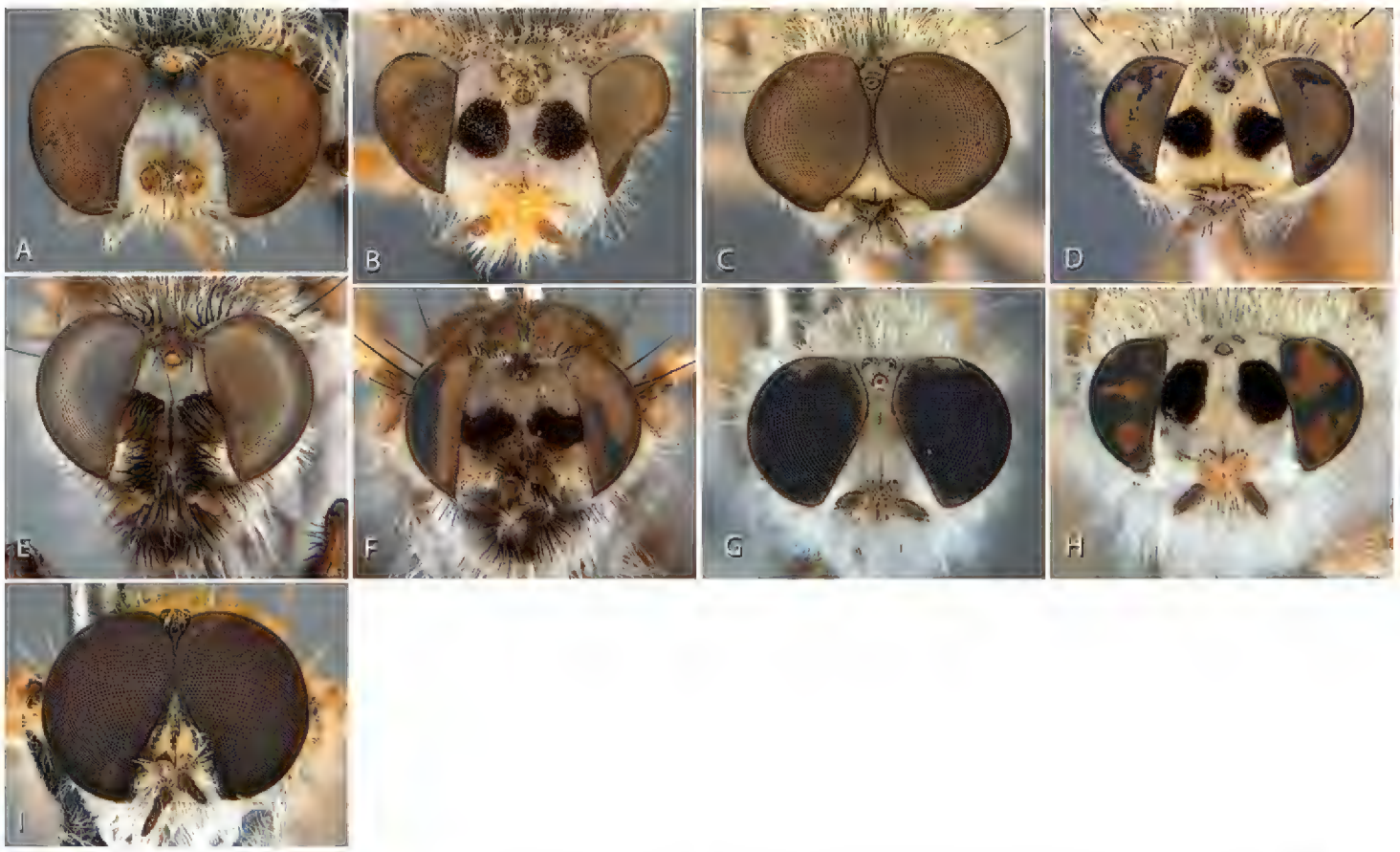

Figure 11. *Neotherevella* species, head, frontal view **A** *Neotherevella kozlovi* (Zaitzev, 1971a), male **B** same, female **C** *Neotherevella arenaria* (Lyneborg, 1976), male **D** same, female **E** *Neotherevella londti* sp. nov., male **F** same, female **G** *Neotherevella macularis* (Wiedemann, 1828), male **H** same, female **I** *Neotherevella maroccanus* sp. nov., male.

yellow; tarsi dark yellow with apices brown; wing opaque white, brown along veins; cell m_3 closed; venation yellow basally along major veins, darker distally; haltere dark yellow; scutal chaetotaxy: notopleural, 3; supra alar, 1; post alar, 1; dorsocentral, 0; scutellar, 2. ***Abdomen***. Male abdomen dark yellow, extensive long, setae, yellow dorsally, white laterally and ventrally; terminalia dark yellow. ***Male genitalia***. Not dissected. Externally, extensive long pale setae; gonocoxite with ridge-like outer gonocoxal process, tuft of elongate setae along ventral part of outer gonocoxal process; inner gonocoxal process narrow, spatulate apically. Female unknown.

Etymology. The species epithet is the adjective latinised version of Morocco.

Distribution. Morocco.

Ecology. Typical of many Therevidae, especially dune-associated species, *N. maroccanus* sp. nov. larvae are found around the bases of plants in dune vegetation, where the larvae predate on soil arthropods amongst the plant roots.

Conservation status. Undetermined; this species is only known from a single specimen from the Erg Chebbi sand dunes, which is a popular tourist destination.

Comments. *Neotherevella maroccanus* sp. nov. is a delicate, distinctively coloured species with an extensive covering of yellow and white pile. It appears closely related to *N. macularis*, sharing features such as a narrow male frons and wing cell m_3 closed. This species is known only from a single male specimen reared from a larva.

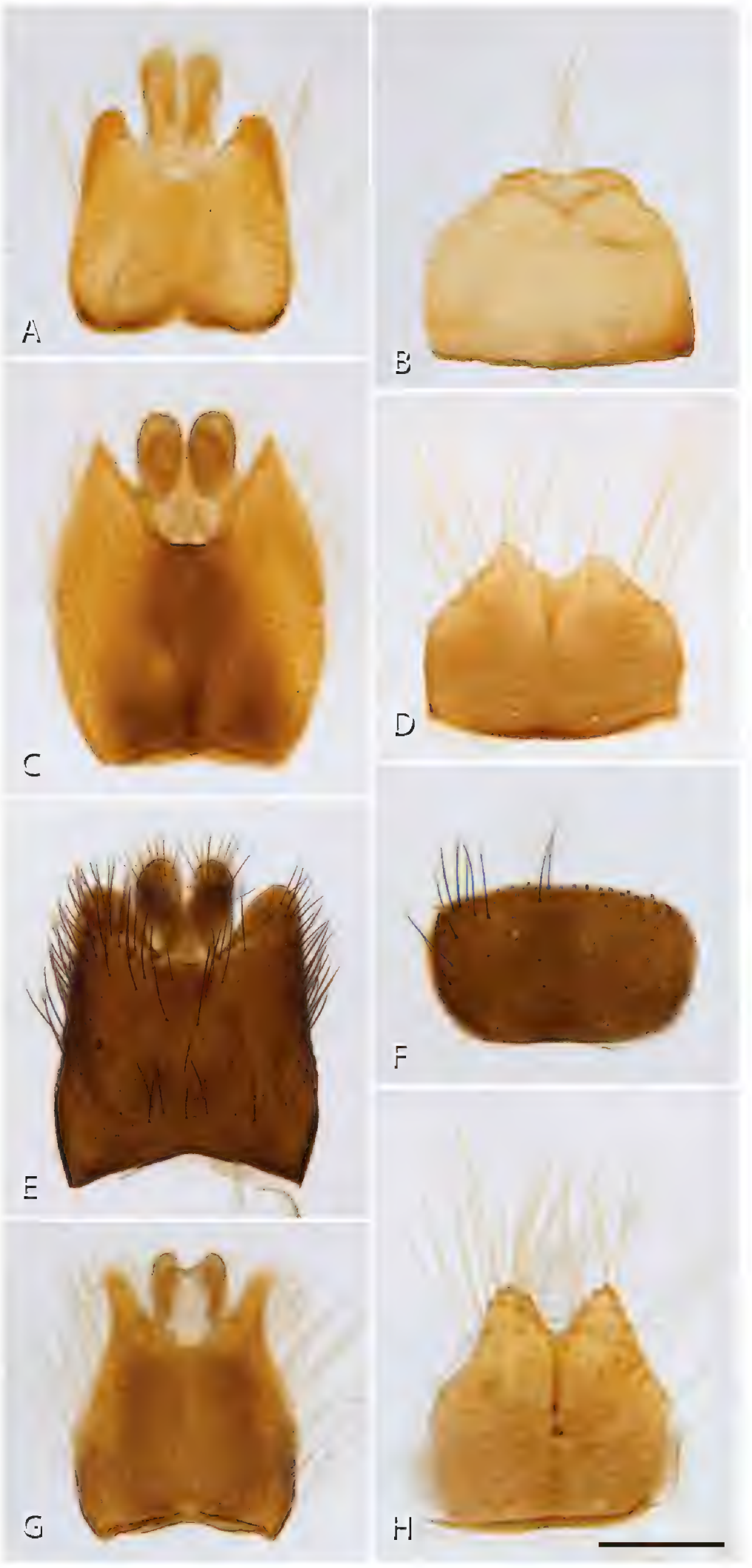

Figure 12. *Neotherevella* species, male epandrium and sternite 8 **A, B** *Neotherevella arenaria* (Lyneborg, 1976) **C, D** *Neotherevella kozlovi* (Zaitzev, 1971a) **E, F** *Neotherevella londti* sp. nov. **G, H** *Neotherevella macularis* (Wiedemann, 1828). Scale bar: 0.25 mm.

Figure 13. *Neotherevella* species, male gonocoxites (ventral view left, dorsal view right) with phallus *in situ* **A, B** *Neotherevella arenaria* (Lyneborg, 1976) **C, D** *Neotherevella kozlovi* (Zaitzev, 1971) **E, F** *Neotherevella londti* sp. nov. **G, H** *Neotherevella macularis* (Wiedemann, 1828). Scale bar: 0.25 mm.

Figure 14. *Neotherevella* species, male phallus **A** *Neotherevella kozlovi* (Zaitzev, 1971), lateral view **B** *Neotherevella arenaria* (Lyneborg, 1976), lateral view **C** *Neotherevella londti* sp. nov., lateral view **D** *Neotherevella macularis* (Wiedemann, 1828), lateral view **E** *Neotherevella londti* sp. nov., ventral view **F** *Neotherevella macularis* (Wiedemann, 1828), dorsal view. Scale bar: 0.25 mm.

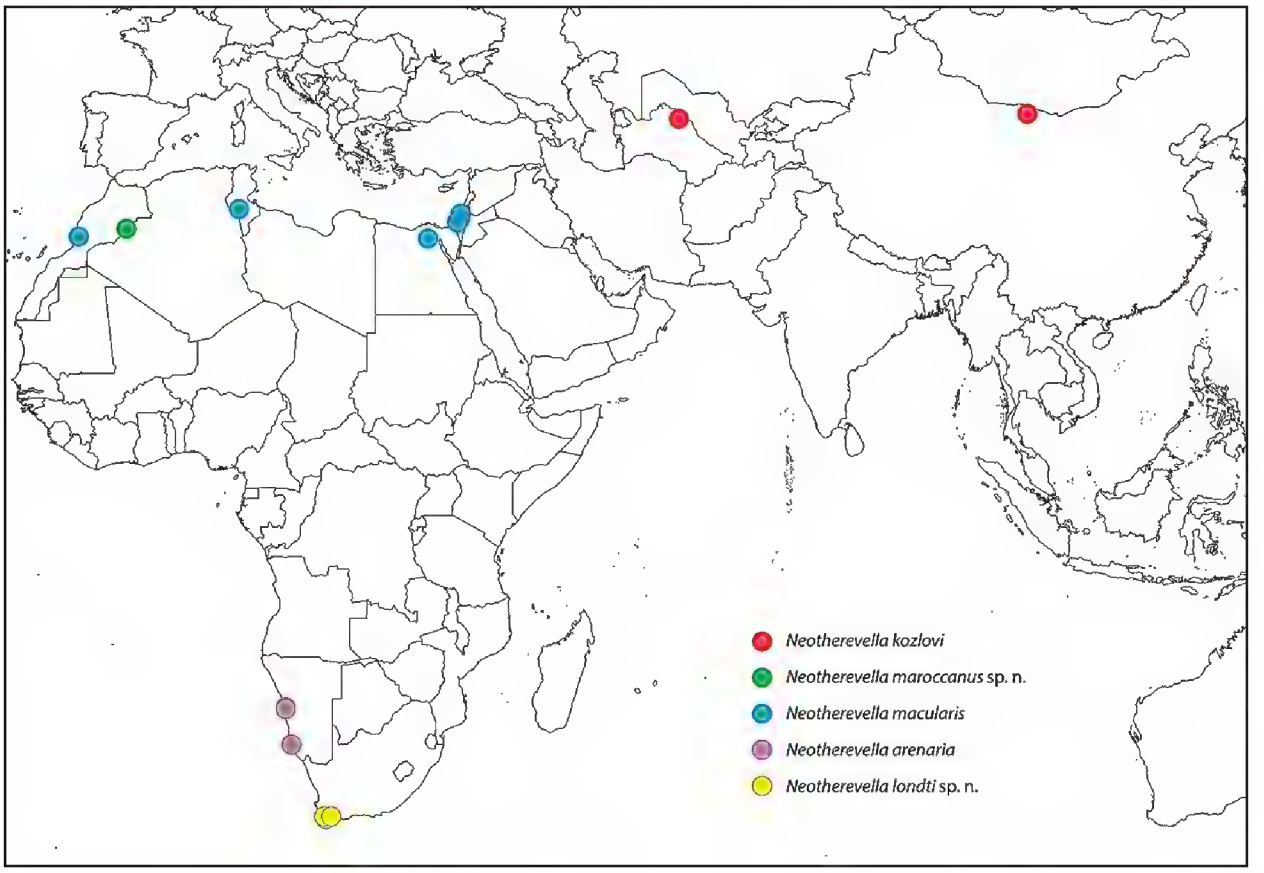

Figure 15. *Neotherevella* distribution.

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References

Becker T (1902) Aegyptische Dipteren. Mitteilungen aus dem Zoologischen Museum in Berlin 2(2): 1–66. [Taf. 4]

Bezzi M (1903) Orthorrhapha Brachycera. In: Becker T, Bezzi M, Bischof J, Kertész K, Stein P (Eds) Katalog der Paläarktischen Dipteren. Vol. 2. Wesselényi, Budapest, 396 pp. https://doi.org/10.5962/bhl.title.5139

Bezzi M (1906) Ditteri eritrei raccolti dal Dott. Andreini e dal Prof. Tellini. Parte prima. Diptera orthorrhapha. Bollettino della Società Entomologica Italiana 37(4): 195–304.

Cumming JM, Wood DM (2017) Adult morphology and terminology. In: Kirk-Spriggs AH, Sinclair BJ (Eds) Manual of Afrotropical Diptera. Pretoria, South African National Biodiversity Institute. v.1, 89–133.

El-Hawagry MSA (2011) Catalogue of Superfamily Asiloidea (Diptera: Brachycera) of Egypt. Efflatounia 11: 1–190.

Frey R (1921) Beitrag zur Kenntnis der paläarktischen Thereviden (Dipt.). Notulae Entomologicae 1: 81–85.

Gorodkov KB, Grunin KJA, Nartshuk EP, Richter VA, Savtchenko, Stackelberg AA, Tanasijthuk VN, Zaitzev VPH (1974) Dipteren aus der Mongolischen Volksrepublik (Diptera, Insecta) Ergebnisse der Mongolisch-Deutschen Bioloischen Expedition seit 1962. Nr. 65. Mitteilungen aus dem Zoologischen Museum in Berlin 2(50): 223–226.

Hauser M, Irwin ME (2003) The Nearctic genus *Ammonaios* Irwin & Lyneborg, 1981 (Diptera: Therevidae). Annals of the Entomological Society of America 96(6): 738–765. https://doi.org/10.1603/0013-8746(2003)096[0738:TNGAIA]2.0.CO;2

Hauser M, Winterton SL, Kirk-Spriggs AH, Holston KC (2017) 49. Therevidae (Stiletto Flies). In: Kirk-Spriggs AH, Sinclair BJ (Eds) Manual of Afrotropical Diptera. Vol. 2. Nematocerous Diptera and lower Brachycera. Suricata (5), SANBI Graphics & Editing, Pretoria, [i–xii +] 427–1361.

Holston KC (2005) Evidence for community structure and habitat partitioning in coastal dune stiletto flies at the Guadalupe-Nipomo dunes system. Journal of Insect Science 5(42): 1–17. https://doi.org/10.1093/jis/5.1.42

Holston KC (2009) A new species of *Acantothereva* Séguy, 1935, from Tunisia (Diptera: Therevidae: Therevinae), taxonomic consequences and phylogenetic implications. Zootaxa 2155(1): 28–36. https://doi.org/10.11646/zootaxa.2155.1.3

Holston KC, Almeida J (2020) First European record for *Acantothereva* Séguy, 1935 (Diptera: Therevidae), with remarks on the western Mediterranean stiletto fly fauna. Boletin de la Sociedad Entomológica Aragonesa 67: 207–210.

Holston KC, Irwin ME, Wiegmann BM (2007) Monophyly and phylogenetic relationships of *Thereva* and therevine genus-groups (Insecta: Diptera: Therevidae) based on EF-1α, 28S rDNA and mitochondrial 16S rDNA sequences. Invertebrate Systematics 21(3): 279–296. https://doi.org/10.1071/IS06005

Irwin ME, Lyneborg L (1981) The genera of Nearctic Therevidae. Illinois Natural History Survey Bulletin 32 [1980]: 193–277. https://doi.org/10.21900/j.inhs.v32.143

Irwin ME, Winterton SL (2020) A new genus of therevine stiletto flies from South America (Diptera: Therevidae). Zootaxa 4838(1): 52–70. https://doi.org/10.11646/zootaxa.4838.1.2

Irwin ME, Winterton SL (2021) Revision of South American stiletto fly genus *Argolepida* Metz & Irwin (Diptera: Therevidae: Therevinae). Zootaxa 5068(2): 151–185. https://doi.org/10.11646/zootaxa.5068.2.1

Kampmeier GE, Irwin ME (2009) Meeting the interrelated challenges of tracking specimen, nomenclature, and literature data in Mandala. In: Pape T, Meier R, Bickel D (Eds) Diptera Diversity: Status, Challenges and Tools. Brill Academic Publishers, Leiden, 407–438. https://doi.org/10.1163/ej.9789004148970.I-459.65

Kertész K (1909) Catalogus dipterorum hucusque descriptorum. Vol. V. Bombyliidae, Therevidae, Omphralidae. Museum Nationale Hungaricum, Budapestini [=Budapest], 199 pp. [+i] https://doi.org/10.5962/bhl.title.5150

Kettani K, Ebejer MJ, Ackland DM, Bächli G, Barraclough D, Barták M, Carles-Tolrá M, Černý M, Cerretti P, Chandler P, Dakki M, Daugeron C, De Jong H, Dils J, Disney H, Droz B, Evenhuis N, Gatt P, Graciolli G, Grichanov IY, Haenni J-P, Hauser M, Himmi O, MacGowan I, Mathieu B, Mouna M, Munari L, Nartshuk EP, Negrobov OP, Oosterbroek P, Pape T, Pont AC, Popov GV, Rognes K, Skuhravá M, Skuhravý V, Speight M, Tomasovic G, Trari B, Tschorsnig H-P, Vala J-C, von Tschirnhaus M, Wagner R, Whitmore D, Woźnica AJ, Zatwarnicki T, Zwick P (2022) Catalogue of the Diptera (Insecta) of Morocco—An annotated checklist, with distributions and a bibliography. ZooKeys 1094: 1–466. https://doi.org/10.3897/zookeys.1094.62644

Kröber O (1912a) Monographie der paläarktischen und afrikanischen Thereviden. (Dipt.). Deutsche Entomologische Zeitschrift 1912(1): 1–32. [part] https://doi.org/10.1002/mmnd.48019120102

Kröber O (1912b) Monographie der paläarktischen und afrikanischen Thereviden. (Dipt.). Deutsche Entomologische Zeitschrift 1912(2): 109–140. https://doi.org/10.1002/mmnd.48019120202

Kröber O (1912c) Monographie der paläarktischen und afrikanischen Thereviden (Dipt.). Deutsche Entomologische Zeitschrift 1912(3): 251–266. [part] https://doi.org/10.1002/mmnd.48019120302

Kröber O (1912d) Monographie der paläarktischen und afrikanischen Thereviden. (Dipt.). Deutsche Entomologische Zeitschrift 1912(4): 395–410. [part] https://doi.org/10.1002/mmnd.48019120202

Kröber O (1913) Diptera. Fam. Therevidae. In: Wytsman PAG (Ed.) Genera Insectorum. 148[me] fascicle. Genera Insectorum, V. Verteneuil & L. Desmet, Bruxelles, 1–62.

Kröber O (1924a) Aegyptische Dipteren aus den Familien der Conopidae, Omphralidae und Therevidae. Bulletin de la Société Entomologique d'Égypte 7: 57–116.

Kröber O (1924b) 26. Therevidae [part 1+2]. In: Lindner E (Ed.) Die Fliegen der palaearktischen Region. Vol. 4(1+2). E. Schweizerbart, Stuttgart, 1–32. [pl. A-C]

Kröber O (1929) Neue Dipteren aus Aegypten aus den Familien Tabanidae, Therevidae, Omphralidae u. Conopidae. Bulletin de la Société Entomologique d'Égypte (N. S.) 13: 73–84.

Kröber O (1932) Familie Therevidae (Stilettfliegen). In: Dahl M, Bishoff H (Eds) Die Tierwelt Deutschlands. Vol. 26(5). Gustav Fischer, Jena, 100–122.

Kröber O (1937) Katalog der palaearktischen Thereviden, nebst Tabellen und Zusätzen sowie Neubeschreibungen. Acta Instituti et Musei Zoologici Universitatis Atheniensis 1: 269–321.

Lyneborg L (1968) The genus *Acanthothereva* Séguy, 1935, with description of a new species from Algeria (Diptera, Therevidae). Mitteilungen der Schweizerische Entomologische Gesellschaft 41(1–4): 298–304.

Lyneborg L (1976) A revision of the therevine stiletto-flies (Diptera: Therevidae) of the Ethiopian Region. Bulletin of the British Museum (Natural History). Entomology 33(3): 189–346.

Lyneborg L (1978) *Neotherevella*, a new genus of Therevidae (Diptera) from the Palaearctic and Afrotropical Regions. Insect Systematics & Evolution 9(1): 75–76. https://doi.org/10.1163/187631278X00241

Lyneborg L (1980) 24. Family Therevidae. In: Crosskey RW, Cogan BH, Freeman P, Pont AC, Smith KGV, Oldroyd H (Eds) Catalogue of the Diptera of the Afrotropical Region. British Museum (Natural History), London, United Kingdom, 314–320.

Lyneborg L (1989) Family Therevidae. In: Soós Á, Papp L (Eds) Catalogue of Palaearctic Diptera. Vol. 6: Therevidae – Empidae. Akadémiai Kiadó [and Elsevier Science Publishers], Budapest [and Amsterdam], 11–35.

Macquart PJM (1848) Diptères exotiques nouveaux ou peu connus. Suite du 2.[me] supplemént [=3rd supplement]. Roret, Paris. 77 pp. [7 pls]

Majer JM (1997) Family Therevidae. In: Papp L, Darvas B (Eds) Contributions to a Manual of Palaearctic Diptera (with special reference to flies of economic importance). Vol. 2. Nematocera and Lower Brachycera. Science Herald, Budapest, 519–529.

Metz MA, Webb DW, Irwin ME (2003) A review of the genus *Psilocephala* Zetterstedt (Diptera: Therevidae) with the description of four new genera. Studia Dipterologica 10(1): 227–266.

Oldroyd H (1968) New Therevidae from Argentina. Journal of Natural History 2(3): 377–385. https://doi.org/10.1080/00222936800770371

Osten Sacken CR (1877) Western Diptera: Descriptions of new genera and species of Diptera from the region west of the Mississippi and especially from California. Bulletin of the United States Geological and Geographical Survey of the Territories 3(2): 189–354. https://doi.org/10.5962/bhl.title.57939

Pyle RL, Michel E (2013) Zoobank: Developing a nomenclatural tool for unifying 250 years of biological information. Zootaxa 1950(1): 39–50. https://doi.org/10.11646/zootaxa.1950.1.6

Steyskal GC, El-Bialy S (1967) A list of Egyptian Diptera with a bibliography and key to families. Technical Bulletin of the United Arab Republic Ministry of Agriculture 3: 1–87.

Wiedemann CRW (1828) Aussereuropäische zweiflügelige Insekten. Als Fortsetzung des Meigenschen Werkes. Vol. 1. Schulz, Hamm., [xxxii +] 608 pp. [7 pls]

Winterton SL (2020) A new bee-mimicking stiletto fly (Therevidae) from China discovered on iNaturalist. Zootaxa 4816(3): 361–369. https://doi.org/10.11646/zootaxa.4816.3.6

Winterton SL, Hardy NB, Gaimari SD, Hauser M, Hill HN, Holston KC, Irwin ME, Lambkin CL, Metz MA, Turco F, Webb DW, Yang L, Yeates DK, Wiegmann BM (2016) The phylogeny of stiletto flies (Diptera: Therevidae). Systematic Entomology 41(1): 144–161. https://doi.org/10.1111/syen.12147

Winterton SL, Irwin ME, Yeates DK (1999a) Phylogenetic revision of the *Taenogera* Kröber genus-group (Diptera: Therevidae), with descriptions of two new genera. Australian Journal of Entomology 38: 274–290. https://doi.org/10.1046/j.1440-6055.1999.00126.x

Winterton SL, Irwin ME, Yeates DK (1999b) Systematics of *Nanexila* Winterton & Irwin, gen. nov. (Diptera: Therevidae) from Australia. Invertebrate Taxonomy 13: 237–308. https://doi.org/10.1071/IT97029

Zaitzev VF (1971a) On revision of the genus *Aristothereva* Frey (Diptera, Therevidae) from Paleoarctic. Communication I. Vestnik Zoologii 1971(3): 63–69. [in Russian]

Zaitzev VF (1971b) On revision of the genus *Aristothereva* Frey (Diptera, Therevidae) from Paleoarctic. Communication II. Vestnik Zoologii 1971(5): 36–42. [in Russian]